

MIGRATIONS OF THE MULTITUBERCULATA AND THE LATE CRETACEOUS CONNECTIONS BETWEEN ASIA AND NORTH AMERICA

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(With 3 figures)

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FOSSIL RECORDS

The Multituberculata are the longest lived order of mammals. If we take into account the records generally accepted as belonging to the Multituberculata, they first made their appearance in the Kimmeridgian and became extinct at the end of the Eocene, which means that they evolved for about 118 million years. It was tentatively claimed by some students of early mammals (Parrington 1967; Hahn 1969; Simpson 1971) that the Rhaetic Haramiyidae are related to the Multituberculata. If we regard the Haramiyidae as the earliest Multituberculata (Fig. 1), the vertical range of this group would be extended to 160 million years.

The time distribution of the multituberculates is usually illustrated in diagrams as a continuous line, extending from Kimmeridgian through Eocene. However, if one combines all known data about the distribution of this group, the line would be broken in several places (Fig. 1). The first gap in the fossil records (if we accept the Haramiyidae as belonging to the Multituberculata) embraces the whole early Jurassic through Oxfordian, which is about 42 million years. The oldest known true multituberculates were found in the Kimmeridgian of Portugal (Kuehne 1961; Hahn 1969, 1971); they embrace three genera, two of which, *Paulchoffatia* and *Kuehneodon*, are assigned to the Paulchoffatidae, suborder Plagiaulacoidea, while *Guimarotodon* is attributed to an undefined family, probably within the Plagiaulacoidea. After Kimmeridgian there is a second gap in the multituberculate time records, which embraces the Portlandian (possibly also latest Kimmeridgian and earliest Purbeckian); its duration was at least 7 million years. The next records are from the Purbeckian of

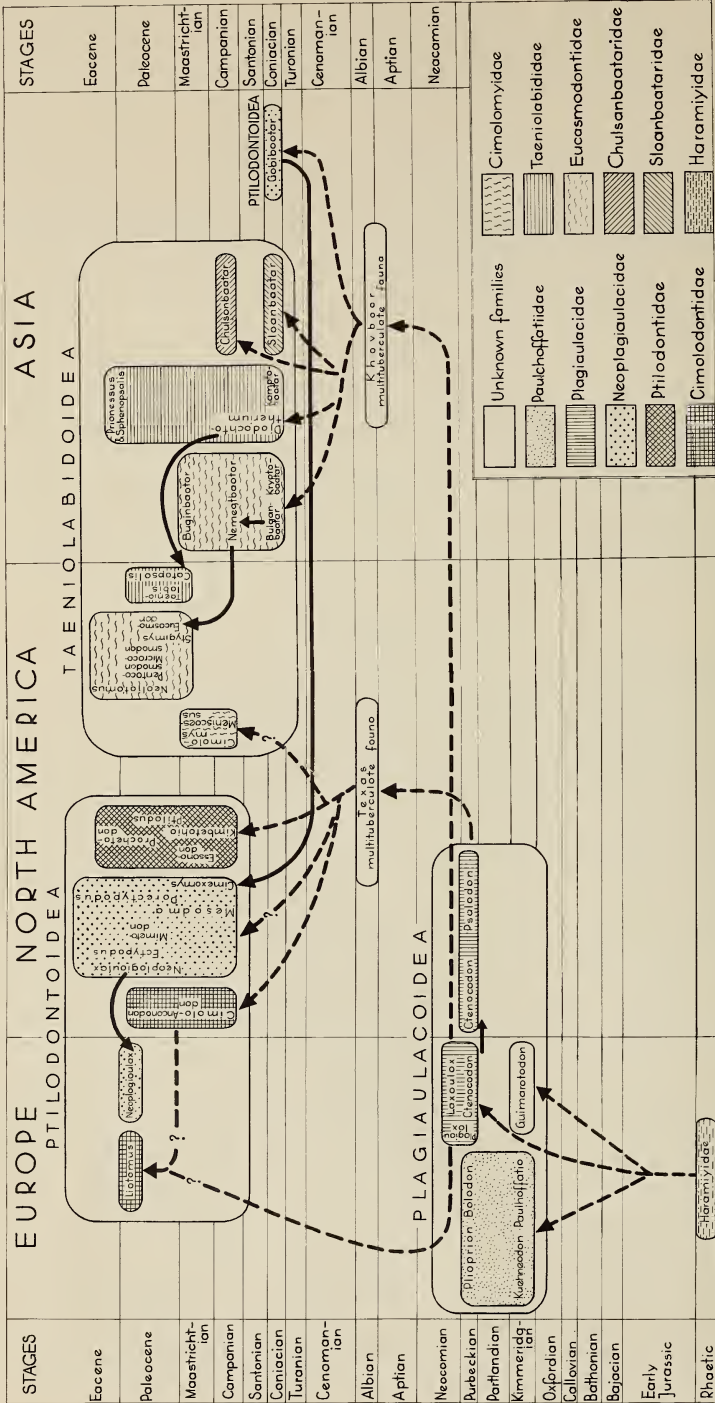


Fig. 1. Geographical and stratigraphical distribution of the multituberculate genera. Each family is marked by a different hatching. The shapes of hatched surfaces are not in proportion to the taxonomic diversity of the families. Discontinuous arrows indicate the probable phylogenetic and migration surfaces are not in proportion to the reasonably well-established migration lines. Stratigraphical ranges of North American genera are based on Sloan & Valen (1966).

Poorly known genus *Vitidomys* from Upper Milk River Formation of Canada is omitted.
 Erratum: read *Paulchoffatia* for *Paulchoffatia*.

Great Britain and from the Morrison Formation of North America, which are probably of the same age. Five genera are known from these beds—the Paulchoffatidae: *Bolodon* and *Plioprion* from Purbeck of Great Britain; Plagiaulacidae: *Plagiaulax* from Great Britain, *Ctenacodon* from Great Britain and North America, and *Psalodon* from North America (Simpson 1928, 1929; Hahn 1969). Of the latest Jurassic genera, uncertain remains of *Plagiaulax* are known from the Wealden of Great Britain, where, in addition, one more plagiaulacid genus *Loxaulax* was found (Woodward 1891; Clemens 1963a). In contradistinction to the Jurassic multituberculates, which are represented by lower jaws with dentition, and in one case also a part of the braincase, the Wealden records are extremely scanty, represented only by a few isolated teeth. After the Wealden there is a third gap in multituberculate records, which extends for the second half of the Neocomian, through the Aptian, and embraces about 15 million years.

In 1969 the Soviet-Mongolian Palaeontological Expedition discovered in the Gobi Desert, at the locality of Khovboor, in Guchin Us somon (county), situated at 102°34 eastern longitude and 45°21 northern longitude, a fauna of early Cretaceous mammals. According to Barsbold *et al.* (1971) the assemblage contains the Multituberculata in addition to the Triconodonta, Symmetrodonta and Insectivora, while according to Kalandadze & Reshetov (1971), in addition to the above mentioned orders, there are also representatives of the Trituberculata. The fauna has not been described as yet and the family assignment of the multituberculates is not known. Barsbold *et al.* (1971) claimed Aptian-Albian as the presumed age of this fauna.

Another early Cretaceous fauna, which is known, but has not been adequately described, is that from the Albian of Texas. Patterson (1956: 9) when describing the Albian fauna from the locality of Forestburg stated: 'Multituberculates are the commonest fossils at Forestburg. . . . All specimens found may be referred to the Plagiaulacidae.' He gave a short description of the Albian multituberculate lower and upper molars, but as the specimens have not been figured, it is difficult to get an idea about their affinities. Slaughter (1965) mentioned some isolated multituberculate teeth in samples from Butler Farm in Texas, which are of the same age as those of Forestburg, described by Patterson. These multituberculates were neither figured nor described by Slaughter.

The fourth gap in the multituberculate record is after the Albian and embraces Cenomanian, Turonian and perhaps also Coniacian, or a part of it, depending on whether the Djadokhta Formation of Asia is of Coniacian or Santonian age. In this discussion let us assume that the Djadokhta Formation is of Coniacian age (Fig. 1). This would mean that the fourth gap in the multituberculate records extends until the end of the Turonian and embraces about 19 million years.

Beginning with the Djadokhta Formation, the multituberculate records are more or less continuous through the Eocene. In the Djadokhta Formation

the representatives of modern multituberculate orders made their appearance: the Ptilodontoidea and Taeniolabidoidea.*

The only representative of the order Ptilodontoidea in Asia is the Djadokhta Formation *Gobibaatar*, assigned to the Neoplagiaulacidae. Four other multituberculate genera recorded from this formation belong to the Taeniolabidoidea; these are *Sloanbaatar*, assigned to the monotypic family Sloanbaatariidae, *Kryptobaatar* and *Bulganbaatar*, assigned to the Eucosmodontidae and *Kamptobaatar* and *Djadochtatherium*, assigned to the Taeniolabididae (Simpson 1925; Kielan-Jaworowska 1969, 1971, 1974). In the younger Asiatic Barun Goyot Formation, which is of Campanian age, the multituberculate fauna so far described consists of three genera: *Chulsanbaatar*, assigned to the monotypic family Chulsanbaataridae, the taeniolabidid *Djadochtatherium*, represented by a more advanced species than its ancestor from the Djadokhta Formation, and the eucosmodontid *Nemegtbaatar*, derived from the Djadokhta genus *Bulganbaatar*. In addition there are in the Barun Goyot Formation three or more, as yet not described, multituberculate genera, none of which appears to belong to the Ptilodontoidea (Kielan-Jaworowska 1974). The post-Campanian multituberculate records are very scanty in Asia. A single genus *Buginbaatar* is known from Bugeen Tsav locality in the Gobi Desert. This is from the beds which are of the late Maastrichtian or early Paleocene age (Kielan-Jaworowska & Sochava 1969). *Buginbaatar* has been tentatively assigned to the ?Cimolomyidae, but in the discussion the authors pointed out (p. 363) that: '*Buginbaatar* n. gen. shares the characters of both the Cimolomyidae and the Eucosmodontidae.' Now it seems more probable to me that it is an eucosmodontid.

The Asiatic records of Paleocene multituberculates are extremely small. Only two taeniolabidoid genera *Prionessus* and *Sphenopsalis* are known from Khashaat (Gashato) and Naran Bulak localities, from beds belonging to either the Paleocene or Eocene (Matthew *et al.* 1928; Szalay & McKenna 1971).

The late Cretaceous multituberculate records in North America begin with the early Campanian Upper Milk River Formation (Fox 1971, 1972). Younger than the Upper Milk River Formation is the Middle Campanian Judith River Formation (Sahni 1972). Beginning with the Judith River Formation there is a nearly continuous multituberculate record in North America through the late Eocene (Granger & Simpson 1929; Jepsen 1930, 1940; Clemens 1963*b*; Lillegraven 1969 and others). The multituberculate assemblages in the Upper Milk River and Judith River Formations are very different from that in the Barun Goyot Formation and in the younger Djadokhta Formation in Asia. In the Campanian of North America, in contradistinction to the conditions in Asia, the Ptilodontoidea prevail over the Taeniolabidoidea.

* In the present paper Sloan & Van Valen's (1965) division of Cretaceous and Tertiary Multituberculata into the Ptilodontoidea and Taeniolabidoidea is tentatively accepted, although I believe that these suborders do not form natural units. The North American taeniolabidoid family Cimolodontidae probably arose independently from the Taeniolabididae and Eucosmodontidae which are of Asian origin. Formal modification of this classification requires, however, a detailed comparative study of North American and Asian multituberculates.

The only taeniolabidoid family represented in these formations are the Cimolomyidae (unknown outside of North America), represented by two genera: *Meniscoessus* and *Cimolomys*. The familial and ordinal assignment of the genus *Viridomys* Fox from the Upper Milk River Formation is uncertain, and that is why *Viridomys* is not shown in Figure 1. In addition to these three genera, in the Campanian of North America three ptilodontoid families are present: the Cimolodontidae, represented by *Cimolodon*, the Ptilodontidae, represented by *Kimbetohia* and the Neoplagiaulacidae (former Ectypodontidae), represented by *Cimexomys* and *Mesodma*. All the multituberculate genera recorded in the Judith River Formation continue through the Upper Edmonton and Lance Formations (Lillegraven 1969; Clemens 1963b) to the latest Cretaceous Hell Creek Formation (Sloan & Van Valen 1965; Van Valen & Sloan 1966). In addition, in Lance Formation the ?ptilodontoid *Essonodon*, which continues through Hell Creek Formation, made its appearance and in Hell Creek the eucosmodontid *Stygimys* and taeniolabidid *Catopsalis* appear.

The above data show that there are no pre-Campanian late Cretaceous multituberculate records in North America. In the Campanian only one taeniolabidoid family, Cimolomyidae, endemic for North America, is present on this continent, accompanied by the representatives of three ptilodontoid families: the Neoplagiaulacidae, Cimolodontidae and Ptilodontidae. By the time of the latest Cretaceous two other taeniolabidoid families, known from older beds of Asia, reach North America: the Taeniolabididae and Eucosmodontidae; while two taeniolabidoid families, the Sloanbaataridae and Chulsanbaataridae, remain so far monotypic and endemic for Central Asia.

The Paleocene and Eocene multituberculate records of North America bring the continuation of the Cretaceous genera and in addition the appearance of new genera in each of the families known in latest Cretaceous on this continent. Within the Neoplagiaulacidae, in addition to *Cimexomys*, which continues in early Puercan, and *Mesodma*, which continues through Clarkforkian (Krishtalka 1973), the four new genera made their appearance: *Mimetodon*, *Ectypodus*, *Neoplagiaulax* and *Parectypodus*, the three latter continuing in the Eocene. One new representative of the Cimolodontidae is recorded: *Anconodon*, while within the Ptilodontidae, in addition to *Kimbetohia*, which continues through Puercan time, two new genera, *Ptilodus* and *Prochetodon*, made their appearance, the latter continuing into the Eocene (Graybullian).

Within the Eucosmodontidae, in addition to *Stygimys*, which continues through the Torrejonian, *Eucosmodon* appears in the Puercan and continues through Torrejonian time, while *Microcosmodon*, *Pentacosmodon* and *Neoliotomus* appear in the Tiffanian, the *Neoliotomus* continuing through the Graybullian.

In the Paleocene the multituberculates appear again in Europe, in France (Russell 1964) and are represented there by the North American genus *Neoplagiaulax* (representative of the Neoplagiaulacidae) and the endemic genus *Liotomus*, assigned by Van Valen & Sloan (1966) to the Cimolodontidae.

DISCUSSION

The data presented above show that during the 160 million years of presumable multituberculate evolution, there are gaps in time records that embrace at least 73 million years. This shows that our information on the development of this group, especially in the first half of its evolution, is extremely scanty.

The oldest Kimmeridgian multituberculates (Hahn 1969, 1971) already show all the essential features of this group. The subsequent evolution concerned only the changes of the dentition, the reduction of the first incisors, the gradual reduction of the premolars and the change of the premolars from chewing into the cutting type. But the essential features of the multituberculate skull and lower jaw structure are already developed by the Kimmeridgian. In the dentary structure there are no great changes between the Kimmeridgian and Tertiary forms. It should be also added that the multituberculate dentary as early as in Kimmeridgian has an entirely mammalian appearance, which is not the case with other groups of mammals from the same beds (Krebs 1971). This shows that the multituberculates are a group which very early branched off from the main evolutionary line of mammals.

All records of multituberculates are confined only to the three continents of the Northern hemisphere: Europe, Asia and North America. The Harniyidae are known from the Rhaetic of Europe—Switzerland and Great Britain (Peyer 1956; Simpson 1928). The Kimmeridgian multituberculates are known also from Europe only, from the single locality in Portugal (Hahn 1969, 1971). In Purbeck time the multituberculate record has been spread from Europe (Great Britain) to North America (Morrison Formation). One genus (*Ctenacodon*) is common for latest Jurassic of North America and Europe, the others are fairly closely related. The earliest Cretaceous fauna (Wealden) is very poorly known and again only from Europe. The above data may lead to the conclusion that the multituberculates originated in Europe.

More detailed data on the evolution of this group have been gathered from the Cretaceous period, particularly so from the late Cretaceous. In the second half of the late Cretaceous the multituberculates were found in two continents: in North America (Albian of Texas) and in Asia (Khovboor locality), the age of which it is either Aptian or Albian. Unfortunately, there are no data about the evolutionary level of the multituberculates at that time, except for the statement of Patterson (1956) that the multituberculates from the Albian of Texas belong to the Plagiaulacidae. It appears from the studies of Hahn (1969, 1971) and others, that of the two plagiaulacoid families, the Plagiaulacidae rather than the Paulchoffatidae are the group which gave rise to the Ptilodontoidea.

The question arises whether in the early part of the late Cretaceous the earliest Ptilodontoidea developed in one part of the globe from the Plagiaulacidae and then migrated to other continents, or whether the different families of the Ptilodontoidea developed independently in various areas. The hitherto recorded data speak rather for the second hypothesis. The oldest known

ptilodontoid is the Djadokhta Formation *Gobibaatar*, belonging to the Neoplagiaulacidae. Unfortunately, the mammals of the same age as those from the Djadokhta Formation are not known from Europe or North America. In the Campanian Upper Milk River Formation, which is the youngest late Cretaceous formation yielding the multituberculates in North America, the Ptilodontoidea are already represented by three families, among the representatives of which only one genus, *Cimexomys*, may be regarded as related to the Asian *Gobibaatar*. All other representatives of the Campanian Ptilodontoidea are much more advanced in structure than the possible Campanian descendants of *Gobibaatar* could be at that time. This indicates that most probably the main stock of ptilodontoid families originated in the first half of the late Cretaceous in North America. Whether *Cimexomys* is a descendant of Asian *Gobibaatar* cannot be asserted with certainty, as the skull of *Cimexomys* is not known and it is difficult to base conclusions on the evolution of multituberculate genera on teeth only. Such possibility is, however, very probable. It is thus an open question whether the Neoplagiaulacidae are a group of monophyletic (Asiatic) or diphyletic (Asiatic and North American) origin.

Nothing can be said about the origin of the North American taeniolabidoid family, the Cimolomyidae. This family embraces two genera: *Cimolomys* and *Moeniscoessus*, which in my opinion are not very closely related to each other. Both are poorly known, we do not know their skull structure and the development of the palate. Therefore it is extremely difficult to discuss their origin, and this question must remain open until more material from this family is collected. As far as the origin of the Taeniolabididae and Eucosmodontidae is concerned, the oldest representatives of both families were found in the Djadokhta Formation of the Gobi Desert. It is very interesting that the Djadokhta eucosmodontid *Kryptobaatar* is extremely similar in the general shape of the skull and in the structure of the cheek teeth to the neoplagiaulacid *Gobibaatar*, which occurs in the same formation (Kielan-Jaworowska 1970, 1974). The differences between the two genera in question concern only the shape of the lower jaw and the structure of the incisors, which in *Gobibaatar* are entirely covered by the enamel, while in *Kryptobaatar* the enamel is restricted to the antero-ventral band. It seems that restriction of the enamel to a band must be considered as the specialized character. It follows that the derivation of Taeniolabidoidea from Ptilodontoidea is theoretically the most probable hypothesis, especially considering the similarity of *Gobibaatar* and *Kryptobaatar*. Even though these two are contemporaries, the ptilodontoid *Gobibaatar* appears to have remained very similar to the forms that gave rise to the eucosmodontid *Kryptobaatar*. In the Djadokhta Formation another eucosmodontid, *Bulganbaatar* also occurs, as well as the oldest representatives of the Taeniolabididae: *Djadochtatherium* and *Kamptobaatar* (the latter genus is very different from *Djadochtatherium*).

The recent findings of a rich multituberculate fauna in the Campanian of the Gobi Desert cast new light on the origin of North American representatives

of the Taeniolabididae and Eucosmodontidae (Kielan-Jaworowska 1974). The eucosmodontid *Bulganbaatar nemegtbaataroides* from the Djadokhta Formation is now regarded as an ancestor of the Campanian (Barun Goyot Formation) *Nemegtbaatar gobiensis*, which seems to be close to the ancestors of the earliest Paleocene North American eucosmodontid *Eucosmodon* (Fig. 2). The

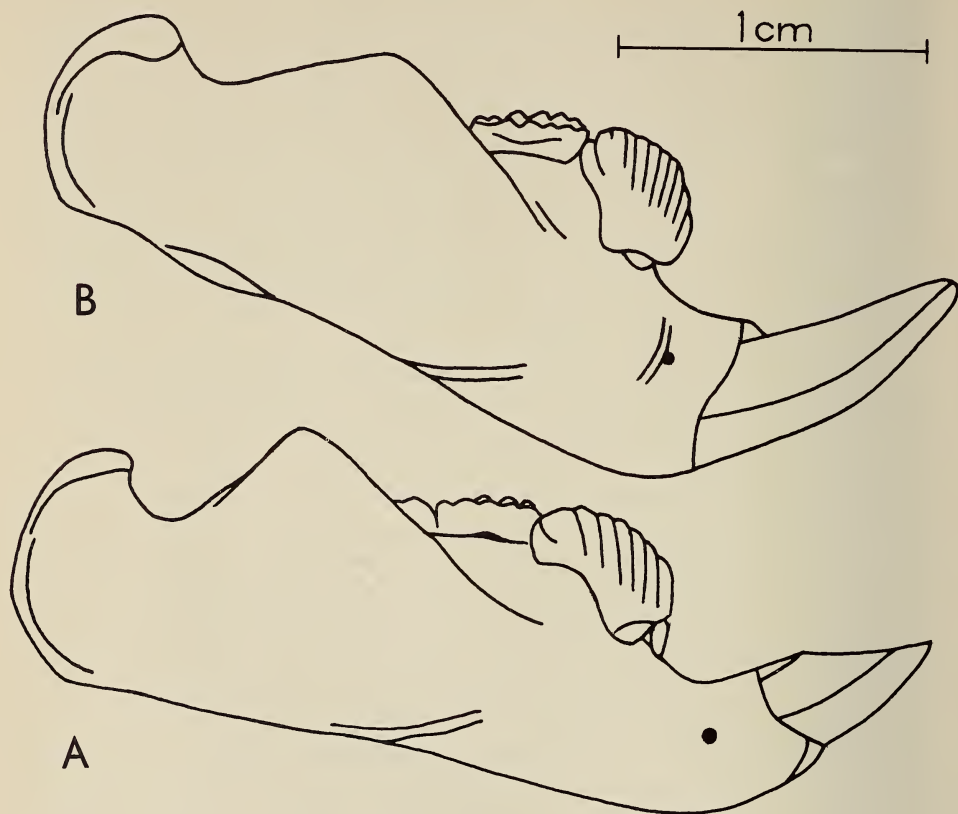


Fig. 2. Comparison of lower jaws in outer view of:
 A. *Nemegtbaatar gobiensis* Kielan-Jaworowska, from the Campanian of Asia. B. *Eucosmodon gratus* Jepsen from the early Paleocene of North America. (A.—After Kielan-Jaworowska 1974. B.—After Jepsen 1940.)

Djadokhta Formation taeniolabidid *Djadochtatherium matthewi* is regarded as an ancestor of the Campanian (Barun Goyot Formation) *Djadochtatherium catopsaloides*, which again is an ancestor of the North American species *Catopsalis joyneri*, known from the latest Cretaceous Hell Creek Formation (Fig. 3).

This indicates that two taeniolabidoid families, the Eucosmodontidae and Taeniolabididae, first developed in the early part of the late Cretaceous in Asia and reached North America in the latest Cretaceous.

Nothing is known on the development of the multituberculates in the

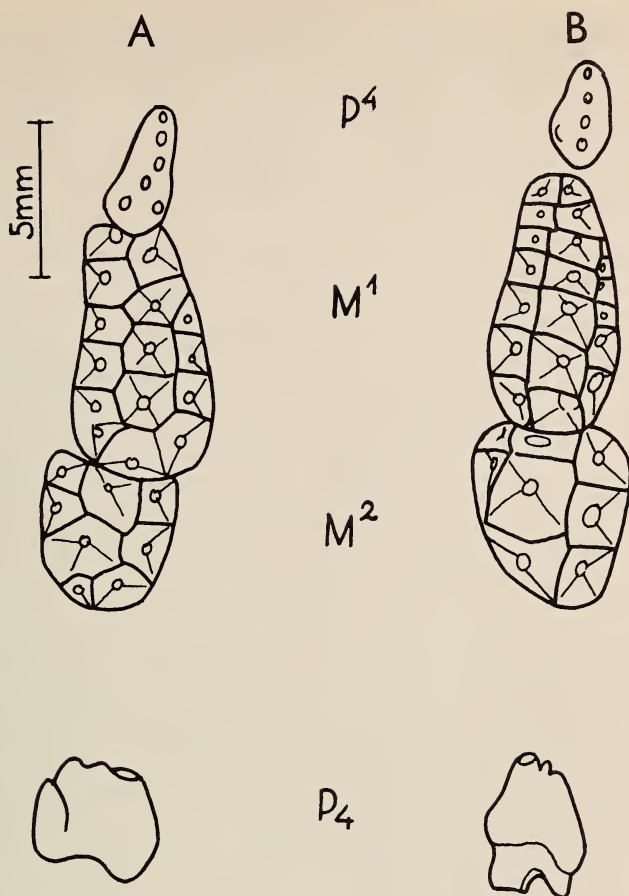


Fig. 3. Comparison of P^4 - M^1 in occlusal view and P_4 in labial view of: A.—*Djadochtatherium catopsaloides* Kielan-Jaworowska from the Campanian of Asia, B.—*Catopsalis joyneri* Sloan & Van Valen, from the latest Maastrichtian of North America. (A.—After Kielan-Jaworowska 1974; B.—After Sloan & Van Valen 1965.)

late Cretaceous of Europe. It is probable that the descendants of European Jurassic multituberculata will be found in Cretaceous and Tertiary strata of this continent. The only known so far early Tertiary representatives of the multituberculata found there, appear to be closely related to the North American forms.

CONCLUSIONS

It appears from the data presented above that in the late Cretaceous three multituberculata lines invaded North America from Asia. One of them (not very certain), the *Gobibaatar* → *Cimexomys* line, belongs to the pre-Campanian

migration, while two others, the *Djadochtatherium* → *Catopsalis* line and the *Nemegtbaatar* → *Eucosmodon* line, belong to the post-Campanian migration. There are no data which indicate that any of the multituberculate groups that flourished in the Cretaceous of North America reached Asia in the late Cretaceous. It follows that in the late Cretaceous the connections between these continents allowed the migration from Asia to North America, but not vice versa.

This conclusion, based on the evolution and distribution of the multituberculates, is partly supported by the data on the distribution of the marsupial and eutherian mammals.

A major component of the North American late Cretaceous mammalian fauna consists of marsupials. As far as the occurrence of marsupials in Asia is concerned, it has been generally accepted until recently that this group never reached Asia. Butler & Kielan-Jaworowska (1973) have shown that two late Cretaceous Asian genera, *Deltatheroides* and *Deltatheridium*, assigned to the Deltatheridiidae, have a marsupial dental formula; however, they classified the Deltatheridiidae as Theria of metatherian-eutherian grade. There is no evidence that any of the late Cretaceous North American marsupials migrated to Asia.

With regard to Cretaceous Theria from North America, Slaughter (1971) believes that among the therians from the Albian of Texas true eutherians occur.

Present knowledge on the early evolution of both eutherian and marsupial mammals is too limited to draw a conclusion concerning the place of origin of both groups. However, even now it can be stated that some of the North American latest Cretaceous eutherian mammals are of Asiatic origin, which has been suggested earlier by Lillegraven (1969).

Simpson (1962) recognized three main paths of faunal interchange for land animals: corridors, filters, and sweepstakes routes. The faunistic differences between Asia and North America in the late Cretaceous are so great that one can reasonably conclude the absence of a corridor. If there was a land connection between these continents one should assume the existence of a filter which prevented the marsupials and certain North American dinosaurs from invading Asia. Such a filter could be the cold climatic zone in north-eastern Siberia, which would be in agreement with the position of the north pole in this region in the late Cretaceous. However, the filter (in Simpson's sense) acts in both directions while the evidence presented in the present paper shows that with respect to mammals this filter acted in one direction only. While the Asiatic multituberculates and eutherians invaded North America, neither the marsupials nor the North American multituberculates reached Asia in the late Cretaceous. The sweepstakes route, in contradistinction to the filter, usually permits rare migrations in one direction only.

An analysis of the late Cretaceous mammalian fauna of Asia and North America leads to the conclusion that these continents were probably separated by a barrier, possibly by marine straits, and the faunal interchange was of the

sweepstakes route type. The existing currents allowed occasional drifts of some invaders from Asia to North America but not vice versa.

The limitation of the present hypothesis is that it is based on the study of the mammals only. Detailed comparisons of other land vertebrates that occur in the Cretaceous of both continents are needed to support or contradict the above hypothesis.

SUMMARY

The stratigraphical and geographical distribution of all described multituberculate genera is discussed. It is shown that the Multituberculata originated in the early Mesozoic in Europe and then migrated to North America and Asia. In the Cretaceous of Asia the Taeniolabidoidea prevail, while in North America it is the Ptilodontoidea. The two taeniolabidoid families: Eucosmodontidae and Taeniolabididae originated in Asia and reached North America in the latest Cretaceous. In addition to the multituberculates, the eutherian mammals migrated from Asia to North America during the late Cretaceous, while the groups of North American origin (e.g. late Cretaceous marsupials and certain multituberculates) never reached Asia. The possibility of a land connection between Asia and North America with a cold zone filter preventing the migration of certain vertebrates is discussed. But inasmuch as the existing barrier, with respect to mammals, allowed one-way migrations only, it is concluded that the faunal interchange between Asia and North America in the late Cretaceous was not of the filter type, but rather of the sweepstakes route type. These continents were probably separated by marine straits and the currents allowed occasional drifts from Asia to North America, but not vice versa.

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ADDENDUM

After this paper was submitted for publication, two papers relevant to the problems discussed herein appeared.

(1) Lillegraven (1972) gives a preliminary description of mammals from the El Gallo Formation (late Campanian) of Mexico. In this paper he described M¹ of ?*Stygimys* sp. This tooth is very similar to that of the Asian *Nemegtbaatar* and probably belongs to the Eucosmodontidae. Be this the case, the Eucosmodontidae should have migrated from Asia to North America at the middle-late Campanian boundary, and not in Maastrichtian as may appear from the data discussed herein and from Figure 1.

(2) Hahn (1973) erects for the Haramiyidae the new suborder Haramiyoidea, within the Multituberculata. This suborder could not be introduced into Figure 1.

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